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The Genesis Kinds: A Perspective from Embryology

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THE GENESIS KINDS: A PERSPECTIVE FROM EMBRYOLOGY

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ABSTRACT
From the days of greatest antiquity, mankind has recognised the distinctive common attributes shared by living things, and has attempted to relate these groups together by devising classification systems - the science of taxonomy or systematics. Much contemporary systematics invokes continuity in order to construct continuous transformational series. By contrast, the taxic or typological paradigm, which can be traced to the pre-Darwinian era, has gained preference over the transformational one in some secular circles [10; reviewed in 42]. This is leading to a systematics independent of evolutionary theory [4]. The types are thus considered as distinct morphological forms, sharing a common structural plan, and in which embryology is of prime concern [59]. Creationists also adopt a typological paradigm, in which the types are identified with the originally-created Genesis Kinds. The contribution of embryology to these issues is here reviewed and assessed. Particular data include hybridisation studies, egg surface structure, cleavage patterns, cell lineage and fate maps, egg capsule structure, larval ontology, sperm morphology and developmental mechanisms.

KEYWORDS
Embryology, Genesis Kinds, Developmental strategy, Cleavage patterns, Cell lineage, Fate maps, Hybridisation.

1. INTRODUCTION
For Charles Darwin embryology was of prime importance in his scheme of evolutionary change [41]. In 1859 he wrote to Hooker [21, p.60] "Embryology is to me by far the strongest single class of facts in favour of change of form." Whilst subsequent evolutionary frameworks have been modified and extended, it remains the case for evolutionists today that the origin and development of morphological diversity is ascribed to embryological processes. Evidence is thus sought for embryonic stages that reflect similarity with a common ancestor. A contrasting paradigm distinguishes distinct types in nature; for creationists, these types can be identified with the originally-created kinds. If such types indeed exist, one might expect to find type-specific characteristics of development, perhaps from even the earliest of stages. It is of interest and intrigue, therefore, to survey and compare development in a range of phyla, to discern which of these models the embryological data may in preference support.

2. BACKGROUND: ORDER IN NATURE
Two contrasting philosophical premises prevail in the search for order in nature. These premises, essentialism and nominalism, were described by Rieppel [42]. Essentialism recognises distinct types in nature. The members of each type all share a common essence. In contrast, nominalism considers the designation of types to be nominal or artificial, and that rather there is a continuous gradation of form among living things.

Essentialism has features in common with the idea of the Biblical Genesis Kinds (Genesis 1:1-27). These Kinds provided a conceptual framework for the most pre-eminent taxonomist, Linnaeus (1707-1778) [31]. Contemporary creationists have indicated the Genesis Kinds to be Basic Types of organisms, each of which may be more equivalent to the higher taxa, such as the family level, than to species. Discontinuities can be recognised between different kinds by a number of criteria e.g. morphology, molecular systematics, hybridisation [39,46,47,48,60,61]. Whilst systematists also employ at least some of these criteria and may recognise discontinuities, creationists consider the discontinuities to be ultimate and unbridgable. Biblical evidence is itself suggestive that the Genesis Kinds represent higher taxic levels than the species [28].

In contemporary literature, structuralists also recognise the essence in organisms [44]. The constancy of structural patterns is seen to result from constrained mechanisms of ontogenesis [52], with such mechanisms designated as the foundation of a taxon [59]. This contemporary renaissance of pre-Darwinian essentialist and taxic frameworks in some circles is an important development, providing stimulating ideas with which creationists can interact. Patterson [38] considered that the transformational approach is dependent on *a priori* hypotheses of transformation which are unobservable; hence, transformational pattern analysis cannot be independent from hypotheses about process. Thus, Darwin explained unity of type by unity of descent. On the other hand, the taxic approach adds the hypothesis of a subordinated, or inclusive hierarchical order [4].

Constraints on form exerted by patterns of development have become the focus of much recent interest [reviewed in 57]. If there are indeed real types in nature, a naturally following hypothesis is that members of a type may share similar mechanisms, structures and factors responsible for the generation of type-specific form [59]. Evidence for ontological manifestations of type- specific forms will now be considered.

3. TYPES: EMBRYOLOGICAL DATA

3.1 **Hybridisation** The literature reveals numerous hybrids observed in nature or captivity. Often the hybrids are not only viable, but fully fertile [33]. The ability to hybridise may reflect common ontogenic pathways and mechanisms. Hybrids are well-documented in taxa such as the following:

a. Approximately one in ten bird species is known to hybridise, and the global incidence could be much higher [33]. Thus, from a world total of 9672 bird species, 895 species are known to have bred in nature with at least one other species [37]. This involves not only interspecific but intergeneric crosses. To this can be added a large number of hybrids found in captivity. Within the family Anatidae (ducks, geese and swans), for example, over 400 interspecific hybrids are known amongst the 150 or so species [46].
b. In the Equidae, out of 15 theoretically possible interspecific hybrids, 14 are known [56].
c. In the Cercopithecidae (old-world monkeys) hybridisations connect eight different genera out of the nine [22].

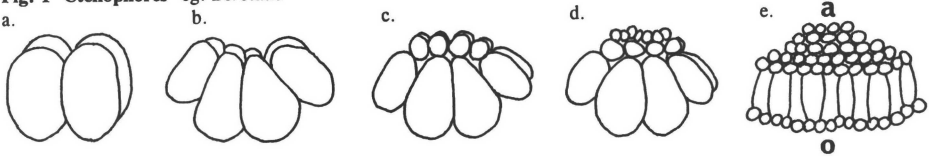
Thirteen potential basic types have been demarcated primarily by using hybridisation data [48]. To this list could be added the Felicidae (cats) and possibly the Ursidae (bears), Cervidae (deer-like) and a considerable number of other bird, mammal and fish taxa (S.E.B. Tyler, unpublished observations).

3.2 **Egg surface topography**
A variety of surface structures such as microvilli, blebs, ridges, folds, ruffles, spikes, and spines, have been observed in the eggs of certain species. The ootaxonomic significance of surface structure is particularly well documented in a number of insect orders [32]. In Gomphinid dragonflies, for example, a hexagonal reticulated surface patterning is seen [1]. Phylogenetically-distinct topographical differences have been evident in the surface architecture of amphibian, molluscan and annelid eggs [cited in 55]. For instance, in gastropod mollusc eggs such as those of *Buccinum*, *Crepidula* and *Nucella* [11], the vegetal pole is characterised by ridges of cytoplasmic outgrowths bearing microvilli. The outgrowths are arranged in a species-specific pattern. Since each of the representatives studied belong to separate families which in turn possibly may be natural types, this vegetal surface architecture may be type-specific. Similarly, the eggs of a few representatives of other phyla have also shown characteristic surface features: nemertines have a conical vegetal protuberance [23]; crustacea show surface sculpturing [40]; cnidaria possess surface microvillous spires [49].

3.3 **Cleavage pattern**
There are a number of notable differences in cleavage patterns, these being conspicuous between various phyla. This is demonstrated by describing a few examples.

a. *Ctenophora* [45]. The first two cleavages are of the usual meridional type (Fig. 1a). The third division is also nearly vertical and results in a curved plate of eight macromere cells (Fig. 1b). The following

Fig. 1 Ctenophores eg. *Beroïdae*



a = aboral o = oral

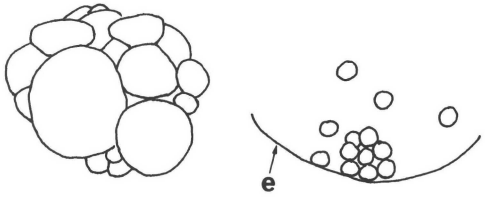
division is latitudinal and unequal, giving rise to micromeres on the aboral, concave side of the macromere plate (Fig. 1c). The micromeres divide several times (Fig. 1d), and the macromeres produce a second set of micromeres at the oral pole (Fig. 1e).

b. *Planaria* [8]. Some in this group exhibit a typically spiral type of cleavage whilst other members show altered spiral, duet spiral, or strongly modified cleavage. Even in the typically spiral type, highly distinctive events occur. Division of the macromeres at the 32-cell stage leads to macromeres remaining at the vegetal pole, which, in spite of their name are minute (Fig. 2a). In the strongly modified cleavage of the rhabdocoels, after the first cleavage, divisions continue randomly until an irregular mass of 80-100 blastomeres is formed. In triclads, the blastomeres become isolated from one another, and are distributed among yolk cells. Yolk cells surrounding the blastomeres fuse to form a syncytium. Meanwhile some of the blastomeres transform into wandering amoeboid cells, migrating to the yolk syncitium (Fig. 2b).

c. *Mollusca* [58]. Mollusc eggs, as in a number of invertebrate phyla, exhibit spiral cleavage, in which each quartet of micromeres is rotated to the right or left of the macromeres in alternate divisions. The first two meridional divisions lead to formation of the A, B, C and D cells. In the following cleavage each of these cells, now called macromeres, divide to form a micromere at the animal pole. This process is repeated to produce further quartets of micromeres, which in turn produce further divisions (Fig. 3).

d. *Arthropoda: Insecta* [29]. Cleavage initially involves several mitotic divisions of the zygote to produce nuclei, some of which migrate to the egg periphery, where mitosis continues. Thus the cleavage nuclei are contained within a common cytoplasm, surrounded only by the egg membrane itself (Fig. 4). Gradually, the egg membrane folds inward to partition off each nucleus into a single cell. Such cells, extending around the embryo circumference, become the cellular blastoderm.

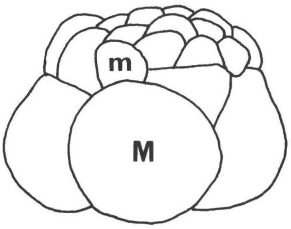
Fig. 2 Platyhelminthes: Planarians
a. *Hoploplana inquilana* b. *Dendrocoelum lacteum*



section through 45-cell stage

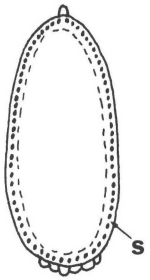
blastomeres (arrowed) migrating vegetally.
e = external membrane.

Fig. 3 Mollusca
eg. *Crepidula fornicata*



sideview of 29-cell stage.
m = micromere; M = macromere

Fig. 4 Insects



s = syncytial blastoderm

Fig.5 Echinoderms: sea urchins

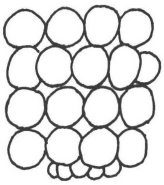
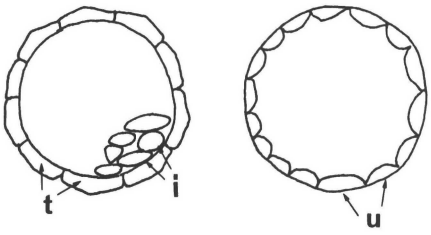


Fig. 6 Vertebrates: mammals
a. eutherians b. marsupials



t = trophectoderm cells
i = inner cell mass cells

u = unilamar blastocyst

e. *Echinodermata* [53]. The first two divisions are meridional, and the third horizontal. In the highly characteristic 4th cleavage, the four cells of the upper, animal layer divide meridionally to form a tier of eight mesomere cells, whilst the lower layer of cells, now known as macromeres, becomes underlain with a tier of tiny micromeres (Fig. 5). In the following division, the mesomere and micromere tiers both divide horizontally, and the macromeres vertically, to produce an embryo of 32 cells arranged in 5 layers.

f. *Vertebrata: Mammalia* Eutherian mammal cleavage is strikingly different from most other patterns of embryonic cell division. During second cleavage, one blastomere divides meridionally and the other equatorially: this is rotational cleavage [20]. Alternatively, both divisions at this stage may be equatorial. Early cell divisions are asynchronous, so that odd numbers of cells are found, rather than the 2- to 4- to 8-cell stages found in other groups. At the 8-cell stage, the cells become compacted, ie. flattened. By the blastocyst stage (Fig. 6a) blastomeres have either differentiated into the trophectoderm cells which contribute the embryonic part to the placenta, or remain undifferentiated in the inner cell mass (ICM) which forms the embryo itself. It is at the blastocyst stage that implantation into the uterus occurs. In contrast, marsupial mammals (Fig. 6b) possess a unilaminar blastocyst with no ICM [50].

3.4 **Cell lineage**

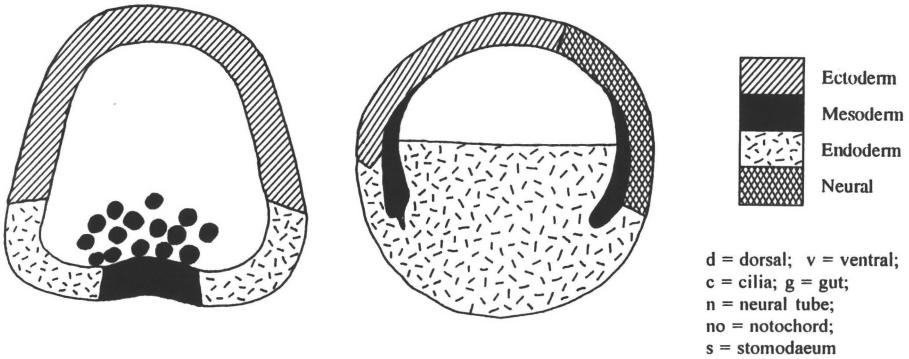
Tracing the fates of cells through development has enabled researchers to establish homologies in different animals [6]. For example, in molluscs the first quartet of micromeres produces the pretrochal ectoderm which in turn gives rise to the head structures such as cephalic eyes, tentacles and cerebral ganglia. The second and third quartet produce the posttrochal ectoderm which includes the somatic plate from which the shell, foot and mantle cavity develop. In the cellular blastoderm of insects, dorsal cells give rise to either dorsal epidermis or an extraembryonic protective amnioserosa, while ventral cells produce the germ band, which in turn gives rise to ventral epidermis, mesoderm and the nervous system. The germ band becomes divided into consecutive metameres corresponding to the definitive body segments. Some embryologists view this uniformity of cell fates as evidence that the taxa sharing this pattern are related in some fundamental way [26]. Fate maps for representatives of 2 phyla are illustrated in Fig. 7. Each map in Fig. 8 is shown at the proposed phylotypic stage (see discussion) for each phylum, when the embryos of various taxa within the phylum may show the maximum similarity [54].

Fig. 7 Fate Maps (vertical sections)

Fig. 7a Echinoderms: sea urchins. Gastrula

Fig. 7b Amphibia: *Xenopus laevis*. Early gastrula

Key to Figs. 7,8. Presumptive Fate regions



d = dorsal; v = ventral;
c = cilia; g = gut;
n = neural tube;
no = notochord;
s = stomodaeum

Fig. 8 Fate maps at phylotypic stages

Fig. 8a Annelids: eg. *Arenicola cristata* Trochophore larva stage

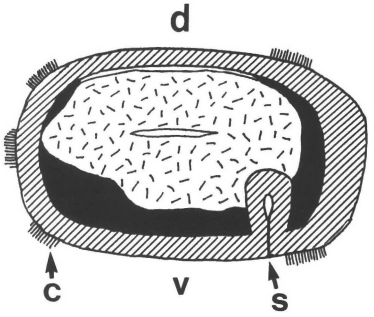
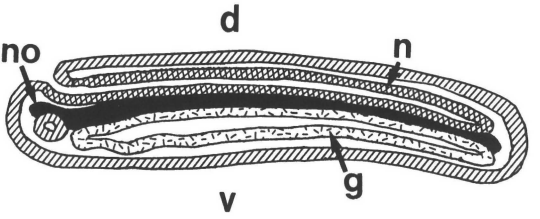


Fig. 8b Cephalochordates, eg. *Amphioxus*: elongation of notochord stage.



(Figs 7,8b after [5]; Fig. 8a after Okada, cited in Kume & Dan [29, p.211])

3.5 Egg capsules

There are other embryological criteria of potential taxonomic significance within particular phyla. For example, the egg capsules (spawn) of some mollusc groups are highly characteristic [43]. The Strombidae (conchs) capsules consist of long, sand-covered tubes of eggs compacted into masses (Fig. 9). The Epitoniidae (wentletraps) have clusters of capsules connected by a single thread like a necklace, and covered with sand. The planktonic egg capsules of the Littorinidae (periwinkles) vary in detail yet have in common a flattish spherical shape overlaid by concentric tiers, or a simplified version of this (Fig. 10). Most of the Naticidae (moon snails) capsules are more or less collar-shaped (Fig. 11). Both structural and behavioural characteristics may together be distinct: for example, the clustered eggs sacs of Calyptraeidae (eg. slipper limpets) are each composed of a delicate, transparent membranous wall, and a narrow stem of attachment to the underlying substrate, and all of which are brooded by the female [14] (Fig. 12); and the Eratoidae (sea buttons/false cowries) and Lamellariidae (ear shells) embed flask-shaped egg capsules within the body tissues of ascidian hosts.

Figs. 9-12 Egg capsules (after [43])

Fig. 9 Strombidae, eg. *Lambis truncata*

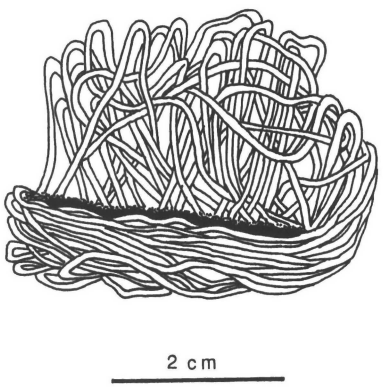


Fig. 10 Littorinidae A. *Nodilittorina pyramidalis*; B. *Peasiella roepstorffiana*

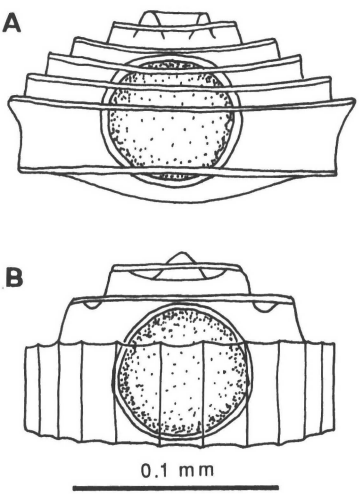


Fig. 11 Naticidae A. *Conuber incei*; B. *Polynices tumidus*

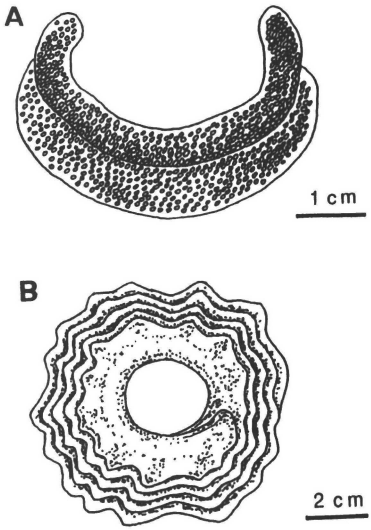
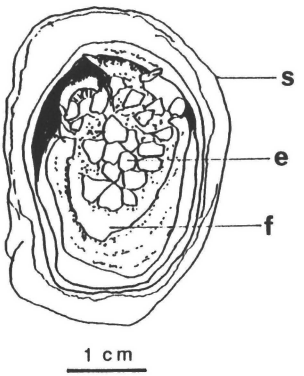


Fig. 12 Calyptraeidae, eg. *Crepidula fornicata* underside of adult female, showing brooding of egg capsules (arrowed)



e = egg capsule; f = foot; s = shell.

3.6 **Protoconch characters**

Certain embryological structures characteristic for a particular phylum may possess variations in ontogenetic behaviour which may be a further aid to their demarkation as types. An example is the mollusc protoconch (larval shell). The protoconch is secreted by an epithelium on the dorsal surface of the embryo known as the molluscan shell field. The comparative embryology of protoconch development was reviewed by Kniprath [30]. For example, most gastropods have helical shells. This form is produced by an accelerated growth of the anterior and of the lateral margins of the shell field. By contrast, in scaphopods (tusk shells), it is the lateral and posterior margins of the protoconch, preceded by similar growth of the shell field, which grow when the lateral ones meet, a tube is thus formed.

Opinions as to the reliability of protoconch characters range from those who thought them to be highly reliable, to those who thought them to be entirely unreliable. The opinions of the former group led to the discrimination of genera based exclusively on protoconch characters. A reason for these opposed opinions is that in some prosobranchs, the protoconch is uniform throughout the whole genera, whilst in other groups there is substantial introgeneric and even intraspecific variation. Many groups do have protoconchs with clearly uniform characters, for example, the Architectonicidae (sundial snails).

3.7 **Sperm morphology**

Within many invertebrate taxa, sperm ultrastructure has been used to deduce phylogenetic relationships. For example, in a study of five families of archaeogastropods molluscs (Haliotidae, Fissurellidae, Trochidae, Turbinidae, and Phasianellidae), it has been found possible to identify members of a family and differentiate between families using sperm ultrastructure [24].

3.8 **Developmental mechanisms**

a. Cytoskeletal behaviour

The cytoskeleton is composed of microfilaments (F-actin filaments), microtubules, intermediate filaments and their associated elements. All of these remain in place to a greater or lesser extent after detergent extraction to remove the cell membrane, followed by washing in physiological saline containing cytoskeletal-stabilising buffers. The elements can be distinguished in electron microscopy by their distinctly-differing diameters.

Comprehensive data for spatio-temporal attributes of cytoskeletal elements throughout early developmental stages is lacking in the majority of phyla, thus making comparisons difficult. However, there are reasonable data for a few groups in the period immediately following fertilisation [reviewed in 12]. This suggests that some organisms use predominantly microfilaments, and others predominantly microtubules

to mediate morphogenetic activities. In annelids, the specification of the polar axis requires the initial segregation of morphogenetic plasms to both animal and vegetal regions of the egg after fertilisation: in *Tubifex* this segregation requires microfilaments whereas in *Helobdella* it requires microtubules. At a similar stage in the nematode, *Caenorhabdites elegans*, microfilaments are required to generate asymmetry. In several species of ascidia, the muscle-forming myoplasm is drawn down into the vegetal region by microfilaments, and then up to the prospective posterior side by microtubules. Just after fertilisation in the amphibian, *Xenopus*, microtubules mediate the cortical rotation of cytoplasm, which determines the future dorsal axis. In the sea urchin, *Hemicentrotus pulcherrimus*, no structural polarity is apparent until after first cleavage, when cortical microtubules appear to mediate the polarisation of surface and cortical regions. In the mouse, polarity only becomes evident at the 8-cell stage, with microfilaments possibly directing the axis of cell polarity. In the mollusc, *Nassarius*, the vegetally-derived polar lobe requires microfilaments and microtubules for lobe formation and resorption respectively, by which the dorso-ventral axis is specified.

b. the cell surface

The development of form, known as morphogenesis, involves a number of cellular structures and processes. If distinct, natural types indeed exist, such structures or processes might also manifest type-specific characteristics. At the molecular level, prime candidates for expressing morphogenetic activity at the surface are glycosylated (carbohydrate-conjugated) proteins and lipids. Their key role in morphogenesis is suggested by the following:

1. They have a potential for encoding a large amount of biological information [3,51]. A vast number of structures can be generated from a small number of saccharide units.
2. Extending outwards from the membrane surface implicates them in adhesion between cells and to the extracellular matrix.
3. A dramatic change in the developmental programme results from the application of glycosylation inhibitors.

Lectins are proteins of non-immune origin, with specific binding sites for particular oligosaccharide structures. They therefore serve as useful probes for the detection and characterisation of surface glycosylated membrane components. For example, the lectin Concanavalin A (Con-A) has a specificity for surface glycoconjugates bearing a terminal mannose or glucosamine. In contrast to the binding of Con-A at the earliest stages of two species of mollusc eggs [12], this lectin does not bind to *Xenopus* eggs and cleavage stages [35], suggesting that either the Con-A receptor has not yet appeared or is masked at these early stages in *Xenopus* development. Particularly interesting is the contrasting behaviour of Con-A binding during gastrulation between representatives in these groups. In the amphibian *Rana* [27], but not the molluscs, a dramatic clustering of Con-A occurs. This behaviour of the Con-A receptors can be correlated with the underlying cellular rearrangements at this stage. The difference between the Con-A binding between the two taxa thus in some way may be related to the profoundly different origins and fates of the various cells between the two groups before and after gastrulation. The lectin-binding patterns in mollusc gastrulation can also be contrasted with the avian pattern [19], in which glucosamine residues are lost just prior to ingression. This may indicate a role of these residues in gastrulation. No loss in lectin binding was observed in molluscs at this stage [12]. The loss of binding of the lectins *Ulex europaeus* agglutinin I (UEA- I) and Con-A in mouse embryos at the compaction stage [62] contrasts with molluscs at an equivalent cell number; throughout cleavage *Nassarius* shows no UEA-I binding and Con-A binding is maintained, and binding of both lectins in *Crepidula* is maintained. The compaction stage is not evident in molluscs. Therefore the difference in binding at the equivalent cell number is consistent with the idea that there are profound differences in development at this stage between these representatives of the mollusc and mammalian taxa.

4. DISCUSSION

In some cases, the embryology of only a few representatives have been studied in characterising a phylum. In other cases, data from a number of subordinate taxa is available, which may be more closely identified with basic types. Even at the phylum level, the embryological data is sufficient for preliminary assessment of its taxonomic implications as follows.

The contemporary evolutionist view of invertebrate origins is typified by Brusca & Brusca [6], who constructed a computer-generated cladogram depicting a proposed monophyletic origin for the metazoa (Fig. 13). However, this scheme is not supported by the data outlined in Section 3, particularly concerning cleavage patterns; cell lineage and fate maps; and developmental mechanisms. Slack [53] emphasised that in a number of groups such as the molluscs, annelids, ascidians and nematodes, the key decisions of early development are made at a very early stage when there are only a few cells in the embryo. The profound significance of early development is apparent from deletion experiments: removal of individual cells from early cleavage stages in determinate embryos such as molluscs leads to loss of adult structures directly derived from these cells. Therefore one is justified in applying early developmental criteria to phylogeny, since it appears that early development is foundational to the morphogenesis of the taxa in

question. Consider then, for example, the emergence of the protostomous platyhelminth, mollusc and arthropod clade from node X on Fig. 13. How can the strikingly different cleavage patterns (Figs. 2,3,4 respectively) and cell lineages exhibited by these groups be reduced to one another? Some planarian platyhelminthes do show features of spiral cleavage in common with those of molluscs. However, in such planaria minute cells are formed at the vegetal pole (Fig. 2a), unlike in the mollusc. Moreover, other patterns are peculiar to planarian groups, namely duet spiral and modified cleavage (Fig. 2b). This can be contrasted again with the syncytial cleavage pattern in insects (Fig. 4). Regarding ctenophores, forming the outgroup at Y in Fig.13, even Brusca & Brusca [6] admit that their development is unique! In comparison of the deuterostome group described, the sea urchin (echinoderm) 32-cell stage consists of five tiers of cells (Fig. 5) resulting from a unique pattern of vertical and horizontal cleavages, and whose subsequent behaviour is peculiar to sea urchins. No such cleavage pattern or series of five tiers are evident in the ascidian embryo at such stages, neither are they seen in any mammals: in eutherian mammals, for example, early cleavage is irregular, and at the 32-cell stage rather than forming five tiers as in the sea urchin, the trophectoderm and ICM can be distinguished (Fig. 6a).

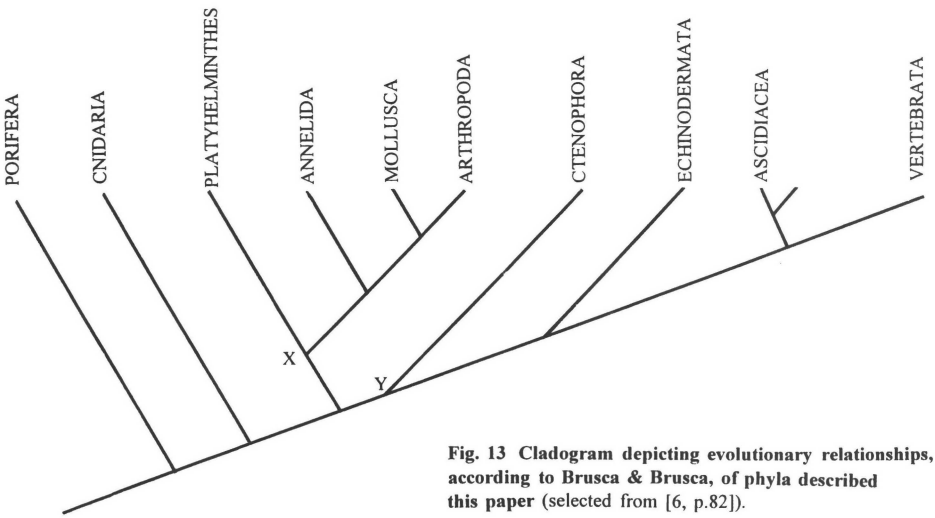


Fig. 13 Cladogram depicting evolutionary relationships, according to Brusca & Brusca, of phyla described this paper (selected from [6, p.82]).

Moreover, fundamental differences in developmental mechanisms are evident in early stages. For example, in ascidians just after fertilisation there is an extensive cytoskeletal-mediated rearrangement of egg cytoplasm, (Section 3.8a) creating distinct cytoplasmic domains unique to this group and which are crucial for later development, including muscle determination. In contrast, such rearrangements are not evident in other deuterostomes such as the echinoderms.

Davidson [9, p.365] has argued convincingly regarding different developmental strategies manifested in various taxa, as is indeed suggested above. He described how spatial patterns may be generated initially: "some embryos begin this process by intercellular interaction, and others even before there are any cells that would carry out such interactions; some rely on lineages that are autonomously committed to given functions as soon as they appear; others deal only in plastic, malleable cell fate assignments; some utilise eggs that before fertilisation are cytoskeletally organised in both axes, some in one axis only, some apparently in neither; for some types of embryos every individual has a different cell lineage, whilst for others there is a set of rigidly reproducible canonical cell lineages; and some embryos display amazing regulative capacities." Thus, he concluded [9, p.366] "the differences among the taxa in their modes of development are anything but trivial and superficial".

Other authors recognise these early differences, but merely relate them to divergence before and after the phylotypic stage stage of embryogenesis, when members of a taxon show maximum similarity, and when the body plan may be generated. Is there evidence for a common ancestry in the phylotypic stages? This has been suggested with reference to a class of genes known as the homeobox, which has been implicated in the specification of relative position within the body. A particular homeobox subset, the *Hox* gene cluster, show a comparable expression pattern in a number of phyla [reviewed in 54]. It has been suggested that the *Hox* and other genes encode relative position in the body form of all animals [54]; this pattern, or zootype, is most clearly expressed at the phylotypic stage. However, the utilisation of the phylotypic stage for hypotheses of evolutionary transformation has its problems. First, the zootype is

claimed to be a system of anterior-posterior information which largely does not code for particular structures. However, a closer look at the fate maps at the phylotypic stage compared between various phyla reveals that the structural differences are profound. For example, consider annelids (Fig 8a) and cephalochordates (Fig. 8b). In the latter, even by this phylotypic stage, chordate structures such as the notochord and dorsal neural tube are apparent, whereas these are absent from annelids at or after the phylotypic stage. In the cephalopods, the notochord develops from mesodermal cells whose origin and cell lineage contrast with that of annelids. Second, developmental mechanisms, such as gastrulation, may also be profoundly different between phyla, and indeed if the phylotypic stages of two groups under comparison are at different developmental stages, it is hardly appropriate to compare their developmental mechanisms, since these are frequently stage-specific. Third, to forward the idea of evolutionary transformation during the phylotypic stage is yet again a case of superimposing it on the data. Equally, stages such as the gastrula (the phylotypic stage of some invertebrates) could be a necessary developmental stage for many phyla, just as is cleavage in all metazoa the means of attaining multicellularity! Thus similarity of stage is not necessarily suggestive of common descent: all other possible pathways may be constrained as forbidden or impossible morphologies. Fourth, interest in the phylotypic stage is primarily because, according to Hall [21, p.98] "the phylotypic stage is a search for the physical embodiment of the link between development and evolution". Thus, a developmental plasticity at this period when the basic body plan may be laid down would be open to the generation of evolutionary novelty. However, this may not be a valid claim. What exactly is meant by the laying down of the body plan? In certain phyla such as the molluscs, necessary antecedants to this stage are demonstratably present in the very earliest of stages, even in the uncleaved egg. Therefore the suggested developmental plasticity at the phylotypic stage may be constrained by earlier formative events. Fifth, caution has been urged by some authors concerning the relationship between homeotic genes and body pattern formation. These genes do not necessarily have the same role in different organisms [34], implying other factors may be important in the generation of type-specific patterns. Indeed, different genetic systems are used in arthropods and vertebrates to regulate the *Hox* complexes. The morphogenetic action for the *Hox* genes remains to be demonstrated. Therefore the sweeping assertion that the zootype - an inter-phyla common expression pattern - embodies a common ancestor, remains unjustified. This is even more the case because the molecular basis for the differences in structure and developmental mechanisms between phyla also remain to be established. It may well turn out to be that such differences cannot be reduced to any common ancestral patterns, but that they nevertheless play a central role in morphogenesis.

Another view is that genes do not so much cause or control morphogenesis; they enable it to take place. Indeed, there is a disjunction between DNA content on the one hand and morphological form on the other [15]. According to Bard [2, p.265-6], there have been few studies where the techniques of molecular genetics have been helpful in elucidating morphogenetic mechanisms. He considered that the results of such techniques have been expressed in genotypic rather than phenotypic terms, and it remains a major project for future work to translate the one into the other. Goodwin [16, p.238] added that an understanding of the sequential action of genes and their products is not a model of morphogenesis. Chemical forces, leading to standing waves of morphogens, do give spatial periodicities of the right wavelength, but these are not equivalent to the mechanical forces that generate cell/tissue shape changes during morphogenetic processes such as segmentation, gastrulation or tentacle formation. The genes may define the parameter ranges for a particular form, but the primary cause of morphogenesis may result from the transmission of stress-strain forces in the surface-cytoskeletal matrix, behaving as a visco-elastic gel. This, according to Oster [36] has the mechanical properties capable of generating form during development. Even advocates of the current "genocentric" position recognise that no genes act in isolation, each functioning within an extensive regulatory cascade [25]. The exquisite nature of regulation and processing of DNA sequences is bringing the cytoplasmic machinery responsible for this increasingly centre-stage. The genome is part of an organisation that is integral with the entire cell, and thus, according to Goodwin [15, p.35] "it is the characteristic dynamic order of the whole process that defines the unique characteristics of organismic form".

A resolution to these contrasting paradigms, or further insight into their explanatory value may be provided by the essentialist approach, which recognises distinct morphological types in nature. The development of form peculiar to each type may be the direct consequence of different strategies. It may thus turn out to be that each type manifests a unique mosaic of strategies, some of which may be evident in other types, but not the whole set [12]. The extensive hybridisation data (Section 3.1) is consistent with this idea: several hybridisation matrices have provided an objective provisional demarcation of basic types. Such hybridisations may be possible only between organisms manifesting common ontogenic pathways.

The concept of a common morphological type persists today as the *Bauplan* (*Bau*, design or type of construction; *plan*, pattern). Eldridge [13] defined the Bauplan as the common basic plan within a monophyletic taxon. Until recently, the idea of a gradual progression of structural complexity from a few simple types in the early epochs prevailed. However, the fossil fauna from the Burgess Shale (Lower to Middle Cambrian Period) contain representatives of every modern phylum except the Bryozoa [7]. Gould

[17] stated that in the 500 million years since the Burgess shale flourished, not a single new phylum, or basic anatomical design, has been added to the Burgess complement. Hall [21] asked why this is so. His solution was that the Bauplan may be protected from selection because of tightly interlocking epigenetic interactions. Thus he envisioned common networks of developmental interactions integrated with epigenetic processes preserving the basic body plans as "types".

If there are fundamental mechanisms of morphogenesis such as the generation of the primary body axis, then how are the differences between forms generated? Should there be type-specific mosaics of developmental mechanisms, then data on such mosaics need to be built up, i.e. to extend the knowledge of surface, cytoskeletal, ionic and electro-physico- chemical structure and behaviour both within and between types. A more complete picture of such mosaics may in turn provide a handle upon any more fundamental, and possibly universal, mechanisms of morphogenesis [12].

5. CONCLUSIONS

Early stages of different phyla can be distinguished by unique patterns of cleavage, cell surface characteristics and cellular morphogenetic behaviour. In addition, other embryological criteria such as sperm morphology and egg case structure show type-specific characteristics. Taken together, these data are consistent with the model that states there are types in nature which originally were created. These embryological data can be used as further criteria in the demarcation of such types. In turn the elucidation of type-specific features in early development may provide a handle upon the fundamental processes of the generation of form, which remain elusive.

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